

Base growth temperatures, germination rates and growth response of contemporary spring wheat (*Triticum aestivum* L.) cultivars from the US Pacific Northwest

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Abstract

In eastern Washington, spring wheat cultivars that germinate and grow fast at low temperatures will provide the crop with a competitive advantage over spring emerging weeds in commercial production fields compared to cultivars that germinate and grow more slowly. The objective of this research was to develop a protocol to identify spring wheat cultivars that would germinate and grow more quickly at low temperatures. A novel data analysis method was used to separate the germination process into three components: (1) base temperature, (2) time to initiation of germination, and (3) germination rate. Spring wheat cultivars Edwall, Vanna, Wawawai, Wampum, Express, and Spillman were assessed through a series of controlled temperature gradient plate experiments. Base temperatures were not different ($P = 0.1$) across cultivars, and once germination was initiated, germination rates among varieties were uniform ($P = 0.5$). However, significant ($P < 0.001$) differences were detected among varieties for time to germination. A subsequent growth chamber experiment confirmed differences in emergence and growth rate among spring wheat cultivars. Published by Elsevier Science B.V.

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1. Introduction

In the Pacific Northwest of USA, spring wheat plants must compete with a variety of summer annual weeds for water, nutrients and sunlight in the field. Significant grain yield losses may result (Cook and Veseth, 1991). Early planting can be used as a cultural method of enhancing the competitiveness of spring wheat against these weeds (Spandl et al., 1999) and if

early planted spring wheat plants gain adequate biomass and the crop canopy fills prior to the emergence of summer annual weeds, they will have a competitive advantage. Unfortunately, low soil and cool air temperatures in the early spring often limit the growth rate of spring wheat, greatly reducing their ability to compete with weeds. Some crop producers in the region are beginning to use direct seeding as a method of soil conservation, further reducing soil temperatures and increasing soil moisture levels in the spring. Planting delays and reduced emergence rates can result (Cook and Veseth, 1991). We developed a selection assay and a nonlinear analysis methodology

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to efficiently identify spring wheat varieties that germinate and grow well at low temperature.

Three principles were basic to this research. First, cultivars have different base temperatures for growth, below which no biological development will occur (Montieth, 1984). Second, time to germination varies among plant biotypes or cultivars (Weaver and Thomas, 1986; Eagles, 1988). Third, differential growth responses to temperatures above the base temperature exist among varieties (Mann et al., 1985). Assuming variation in base temperature, time to germination, and growth response to temperature among spring wheat biotypes, opportunities for developing varieties that grow faster at low temperature may exist.

Seed germination and early plant growth are complex processes dependent on the interaction of soil temperature and soil moisture, as well as photoperiod (Montieth, 1981). With adequate moisture and optimal photoperiod, base temperatures have been estimated for a wide range of plant species (Bierhuizen and Wagenvoort, 1974; Del Pozo et al., 1987; Roché et al., 1997a,b). Base temperatures are often determined by an extrapolation of germination rates over a range of temperatures (Montieth, 1981; Garcia-Huidobro et al., 1982; Del Pozo et al., 1987). The extrapolation is generated either from a linear or quadratic equation obtained by plotting temperature against the reciprocal value of time (Bierhuizen and Wagenvoort, 1974; Montieth, 1977; Lawlor et al., 1990; Roché et al., 1997a).

Germination begins when an imbibed seed is exposed to temperatures above the base temperature (Montieth, 1981). Germination rate is temperature-dependent, with increased germination rate at warmer temperatures. However, when expressed in terms of growing degree days, or heat units, the rate of germination has proved to be similar until a maximum temperature is reached (Montieth, 1981). Several models proposed to represent the germination process have been reviewed by Brown and Mayer (1988) who found the Weibull function (Weibull, 1951) most satisfactory. This function derives an equation to describe development times based on a single temperature-independent distribution that is representative of all normalized distributions measured over a range of temperatures. The Weibull function also has been used to describe insect development over time (Wagner et al., 1984), as well as seed germination and

bud break (Bridges et al., 1989; Holshouser et al., 1996). Unfortunately, none of the reviewed models estimate base temperatures for growth.

Breeding for improved germination rates at low temperatures has been successful for beans (Dickson, 1971), tomatoes (Cannon et al., 1973; De Vos et al., 1982; Scott and Jones, 1985), maize (Eagles, 1988), and cotton (Marani and Dag, 1962). Chilling sensitivity tests have been developed for maize (Hodges et al., 1994, 1995) and soybean (Bramlage et al., 1979). Based on the results of these studies and the perceived competitive advantage in the early establishment of a wheat crop, we developed a method to identify spring wheat cultivars that germinate at low base temperatures and grow in the cold. White and red seed types were compared, as the red seed type is associated with a dormancy factor that may impact germination (Warner et al., 2000). The objectives of this research were to (1) develop a protocol to test the low temperature germination ability of spring wheat cultivars and (2) develop a quantitative method for comparing base temperatures and germination rates of crop plants.

2. Materials and methods

2.1. Temperature gradient plate experiment

Similarly sized seed of six spring wheat cultivars produced in the same crop year were obtained from the Spring Wheat Breeding and Genetics Program at Washington State University. Three of the cultivars ('Edwall', 'Vanna', and 'Wawawai') were soft-white spring wheat varieties; the other three ('Wampum', 'Express', and 'Spillman') were hard red spring varieties. All six varieties are currently grown commercially in the Pacific Northwest of USA. Edwall, Wawawai and Express are early maturing varieties; Vanna, Wampum and Spillman flower late. Wawawai and Wampum are tall, and Edwall, Express, Vanna and Spillman, are standard height varieties (Miller et al., 1997).

Three locally built temperature gradient plates based on a design by Larsen (1962) were used to assess germination rates among cultivars. The gradient plates were calibrated for a similar temperature range, consisting of six specific temperature grids (6.4, 10.0, 13.1, 15.7, 20.2 and 25.2 °C), using a surface thermometer,

accurate to 0.1 °C. Six germination paper disks (8.5 cm diameter) were placed on each temperature grid (one for each cultivar) with 50 seeds per disk. The germination paper and seeds were wetted with distilled water and covered with petri dish bottoms to reduce evaporation. Distilled water chilled to the specific temperature of each grid was applied as necessary to keep the germination paper moist. Radicle emergence, radicles ≥ 10 mm, and shoots ≥ 10 mm for each seed sample \times variety \times temperature treatment were recorded every 12 h for 21 days. Once a seed had successfully met all three conditions, it was counted as successfully germinated and removed.

The original experimental design was a 6×6 (spring wheat cultivars \times temperatures) Latin square on each of the temperature gradient plates (Steel and Torrie, 1980). However, when, initial data analysis of results detected no evidence of any systematic effects within a temperature across a plate, but marked temperature effects across plates, the data were analyzed using a split plot design (Steel and Torrie, 1980).

For each of the 108 plate \times temperature \times variety combinations tested, the following model was fitted to the percent germination data:

$$p(t) = \begin{cases} 0, & \text{if } t \leq k \\ 100(1 - r^{t-k}), & \text{if } t > k \end{cases} \quad (1)$$

where $p(t)$ is the function of the percent germination over time, t is time, k is time at which germination begins and r is the slope factor. The estimates of k and r from this model were then analyzed using standard analysis of variance (ANOVA) methods for a split plot (Genstat 4.1). For this it was necessary to log transform the data (after subtracting 1 from r to remove values of 0). The results presented are the back-transformed means, re-scaled so that their overall mean equals the overall mean of the untransformed data. Because of the back transformation to the original scale using antilogs, values are now geometric means, and the least significant difference (LSD) of the transformed data become the equivalent of least significant ratios (LSRs) (Steel and Torrie, 1980). Estimates of base growth temperature were obtained by fitting a smoothing spline to $1/k$ for each plate \times variety combination using the Bayesian program Flexi (Upsdell, 1994). The resulting estimates were then analyzed by ANOVA methods for a split plot (Genstat 4.1).

2.2. Growth chamber experiment

A growth chamber evaluation (15 °C and a 16 h:8 h day:night temperature ratio) was conducted to determine whether germination results from temperature gradient plate analyses applied to seeds of each variety planted in soil. The growth chamber temperature was selected based on results of the temperature gradient plate which measured the greatest differences near 15 °C. Fifty seeds of each spring wheat variety from the previous study were sown 2 cm deep into 3 l pots with four replications per variety. The potting medium was a soil mixture of 60% peat, 20% pumice and 20% sand and pots were watered as needed. Emergence was recorded daily, and after 2 weeks, all seedlings were cut at ground level for plant height and dry weight determination. The experimental design was a completely randomized block with four replications. Data were evaluated through ANOVA, and LSD at the 5% probability level was used to compare cultivar means (Genstat 4.1).

3. Results and discussion

3.1. Temperature gradient plate experiment

Base temperatures about which plant growth can be initiated are quite variable among crop species, with estimates of 2.6 °C for wheat and 9.8 °C for maize (Angus et al., 1981). Among the six spring wheat varieties tested, no significant differences ($P = 0.1$) in base temperatures, which ranged from 1.2 to 1.6 °C, were detected. This difference in base temperature compared to the work of Angus et al. (1981) may be due to the fact that the wheat cultivars they tested had been selected for the warmer climate of Australia, where the ability to grow at colder temperatures does not impart an advantage as it would in the Pacific Northwest of USA. The difference could also be due to methodology.

As a group of seeds begins to germinate, one is interested in the time it takes for all the viable seeds to germinate. This time is represented by r in Eq. (1). Within a temperature, no significant differences ($P = 0.5$) in the slope factor r among varieties were detected (Table 1). Thus once germination was initiated, the rate of germination at a given temperature did not vary among varieties. However, significant differences

Table 1

Values of r (the slope factor) from Eq. (1) for seeds from six spring wheat varieties germinated at six temperatures on a temperature gradient plate^a

Temperature (°C)	Variety					
	Edwall	Vanna	Wawawai	Express	Spillman	Wampum
6.4	0.99	0.98	0.99	0.99	0.99	0.99
10.0	0.97	0.97	0.98	0.98	0.97	0.98
13.1	0.94	0.97	0.98	0.96	0.97	0.98
15.7	0.95	0.94	0.96	0.96	0.95	0.95
20.2	0.89	0.90	0.92	0.94	0.92	0.91
25.2	0.85	0.89	0.92	0.87	0.85	0.88

^a LSR at 5% confidence level is equal to 1.59 among varieties within temperatures.

between temperatures across varieties were detected, with the rate of germination increasing as the temperature increased (as r decreases the germination rate increases). Overall, the rate of germination at 20.2 and 25.2 °C were faster than that for any of the lower temperatures. Therefore these varieties will germinate at a uniform rate once germination is initiated given similar temperatures.

The time at which germination began, as defined by when both the emerging radicle and coleoptile had reached 10 mm, varied among temperatures and among varieties within a temperature (Table 2). Time to germination was significantly different for each variety at 6.4, 10.0, 13.1, 15.7, and 20.2 °C. Only Wawawai was significantly different from its time to germination at 20.2 °C compared to 25.2 °C. With the exception of the two highest temperatures, the time to initiation of germination decreased as temperature increased. At the three lowest temperatures (6.4, 10.0, and 13.1 °C), no significant differences among

time to germination among varieties were detected. At 15.7 °C Vanna initiated germination earlier than Spillman and Wawawai. At 20.2 °C Vanna and Wampum initiated germination earlier than Spillman and Wawawai. At 20.2 °C Edwall and Express also initiated germination earlier than Wawawai. At 25.2 °C Vanna initiated germination earlier than Spillman and Wawawai. At the higher temperatures, Vanna germinated the earliest, whereas Spillman and Wawawai always germinated last. Among the varieties tested, significant variation was detected in the time required for germination to begin. Based on these results, variation suitable for manipulation through variety improvement strategies exists among this germplasm. Therefore it may be feasible to develop spring wheat varieties with reduced germination time requirements. Time to the initiation of germination was not related to seed coat color as Vanna, the earliest to initiate germination, and Wawawai, often the last to emerge, are both soft-white wheat cultivars.

Table 2

Time (h) that germination began (k in Eq. (1)) after spring wheat caryopses were imbibed and maintained at six different temperatures on a temperature gradient plate^a

Temperature (°C)	Variety					
	Edwall	Vanna	Wawawai	Express	Spillman	Wampum
6.4	264	257	282	274	266	255
10.0	160	143	162	150	151	160
13.1	113	114	117	118	115	105
15.7	90	79	94	87	94	90
20.2	66	60	76	65	72	62
25.2	62	55	64	59	65	61

^a LSR at 5% confidence level is equal to 1.13 among varieties within temperatures.

Table 3

Spring wheat variety emergence values 3–5 DAP^a and development 14 DAP in a growth chamber set to 15 °C^b

Variety	Emergence (%)			Plant height (cm)	Plant dry weight (mg)
	3 DAP	4 DAP	5 DAP		
Vanna	8.3 A	78.1 A	91.1 A	23.0 B	38.3 B
Wampum	4.8 AB	75.1 A	93.1 A	26.1 A	45.7 A
Spillman	1.9 B	40.9 B	80.6 B	22.5 BC	35.5 B
Edwall	1.6 B	82.4 A	97.3 A	22.3 C	38.2 B
Wawawai	1.1 B	53.7 B	92.9 A	22.3 C	37.0 B
Express	0.5 B	58.4 B	90.7 A	22.2 C	38.2 B

^a Days after planting.^b Means within a column followed by the same letter are not significantly different at the 5% level as determined by an LSD test.

3.2. Growth chamber experiment

As determined in the temperature gradient experiment, Vanna, which rapidly initiated germination, was the first to emerge followed by Wampum, whereas Spillman and Wawawai, which took longer to initiate germination in the temperature gradient experiment, were the slowest to emerge (Table 3). By 5 days after planting (DAP), all varieties except for Spillman had reached 90% emergence based on number of seeds planted. Final emergence rates did not differ significantly among the six varieties, ranging from 96 to 100% (data not shown). Growth chamber results supported the findings of the temperature gradient study in that both methods detected significant differences and similar trends among varieties in time to germination and emergence.

Based on plant height and plant dry weight values, Wampum was tallest and generated more biomass than the other varieties (Table 3) after 2 weeks of growth. Vanna and Spillman were the next tallest, but Spillman had the lowest dry weight of the six cultivars (Table 3). At maturity Wampum and Wawawai are the tallest lines in the field.

The results of the growth chamber experiment confirmed those of the temperature gradient plate in that Vanna and Wampum germinated first in both assays at approximately 15 °C, whereas Spillman germinated and emerged last. This temperature is a common springtime temperature in the Palouse region of the Pacific Northwest where these cultivars are typically grown. After emergence, Wampum grew the most quickly and was taller and generated more biomass than did the other spring wheat varieties. This rapid

germination and growth may translate into a wheat plant that is more competitive against weeds (Ogg and Seefeldt, 1999). Additional experiments to assess the competitive ability of these varieties under field conditions are required to confirm this hypothesis.

Our analysis methodology provided very good estimates of base temperatures, time to germination and subsequent rates of germination of spring wheat seeds. With the incorporation of back transformation and the use of LSR, the results are immediately understandable to the layman. These estimates, which were based on temperature gradient plate experiments, were accurate in predicting rates of emergence from pots in a growth chamber. We believe this methodology will work well with other plant species.

Our results have shown that variation exists for low temperature germination ability in spring wheat cultivars in the Pacific Northwest of USA. Further research will be needed to determine the genetic control of the trait and how it can be selected using this methodology.

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